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Phrynosoma m'callii Pertinent to its Systematic Status

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A Study of the Osteology and Musculature of *Phrynosoma m'callii* Pertinent to its Systematic Status

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Since the original description of the flat-tailed horned lizard *Phrynosoma m'callii* (Hallowell) in 1852, there has been considerable difference of opinion as to the generic status of this species. That the matter has not been satisfactorily settled is partly due to insufficient material for skeletal analysis. We have undertaken a study of the pertinent aspects of the osteology and musculature of the head region of *Phrynosoma* and thus are able to present certain facts necessary for evaluation of past study upon *P. m'callii* and speculation concerning its proper systematic position.

The genus *Phrynosoma* was first established by Weigmann (1828) when he split the horned lizard group from the genus *Agama*. *P. m'callii* was first described by Hallowell (1852) who proposed for this form the monotypic genus *Anota*, for the reason that, unlike the lizards of the genus *Phrynosoma*, it lacked external auditory meatuses. In 1858 Girard placed *Anota* in synonymy as he considered the name occupied. He proposed a new genus *Doliosaurus*, to include *P. m'callii* and two other species. Subsequently Cope (1867) placed the flat-tailed horned lizard in the genus *Phrynosoma* only to split it off again (1900) together with four other forms into the resurrected genus *Anota*. This was done mainly on the basis of concealment of the tympanum in all five forms, but was not generally followed because of wide differences within Cope's group.

Bryant (1911) placed *P. m'callii* in the monotypic genus *Anota*. He based this action mainly upon closure of the supratemporal fossae by bone, in the single specimen he had at hand. This arrangement was not followed by Van Denburgh and Slevin (1913) and others, although in 1921 Stephens again

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used *Anota* for the flat-tailed horned lizard. **H. M. Smith** (1946, p. 288) discusses the problem:

"Bryant (Calif.) has shown good reason to believe that the species *m'callii* should be separated from *Phrynosoma*, into a special genus *Anota*, because of the absence in it of a supratemporal fossa. The only reason this is not followed here--and perhaps why other authors since 1911 have not used *Anota* for *m'callii*--is that Bryant's work was based on a single skeleton. An interesting problem presents itself here, for should an examination of several skeletons of *m'callii* prove the invariability of the character, it should be accepted as a generic character, and *Anota* should be recognised."

The authors collected fourteen specimens of *P. m'callii* during the spring of 1947, the spring and summer of 1948, and the spring of 1949. These animals were all obtained in the Coachella Valley, near Palm Springs, Riverside County, California. **In** addition, we have had available preserved material collected at the same locality on earlier dates.

The skulls of *P. m'callii* were dissected out in preference to other methods of skeletonization which do not serve as well to keep cartilage intact. One adult specimen was cleared and stained with Alizarin Red S. In addition, for comparison, skulls of the following species of horned lizards, collected by the authors, were also prepared by dissection: *P. coronatum blainvillii*, *P. cornutum*, *P. douglassii bernandesi*, *P. modestum*, *P. platyrhinos*, and *P. solare*. Two heads of *P. m'callii* were decalcified and sectioned in different planes through the fossa in an attempt to clarify the relationship of the bony shelf to the covering membrane.

Since the structure of the tympanum was used by Hallowell (1852) and by Cope (1900) to define the genus *Anota*, an examination of this structure was also made. Two desert forms, *P. m'callii* and *P. platyrhinos*, were examined in this phase of the study. During the course of the dissections of the tympanum certain differences in neck musculature were noted between *P. m'callii*, *P. platyrhinos*, and *P. coronatum*.

COMPARISONS

Supratemporal fossae. The supratemporal fossae of adult *P. m'callii* are roofed over in variable degree by converging shelves of bone. These shelves are apparently progressive ossifications converging from the three bones that surround the fossae; the postorbital bone on the anterior margin, the supra-occipital bone limiting the fossa medially and posteriorly, and the supratemporal bone bounding the fossa on its lateral edge. In general the largest part of the shelf is formed as an outgrowth from the postorbital bone. The supra-temporal bone contributes the least. The ossification seems to progress within the membrane that covers the fossa. This membrane has been found in *all* species of the genus *Phrynosoma* that have been examined (Fig. 1).

The ten skulls of *P. m'callii* examined proved to be highly variable with regard to percentage of closure of the fossae by bone. In three specimens the fossae are completely occluded. We have examined the specimen used by Bryant (1911) in his study and it is included in this group with completely occluded fossae. Three individuals possess fossae that are two-thirds to four-fifths covered by bone, and two animals fall in the class with fossae one-third to one-half covered. All of these (9) specimens are adults. The considerable range of variation in the adult age group is further indicated by the following: adults with snout-vent lengths of 80.5 mm., 79.2 mm., and 78.7 mm. show respective fossae occlusions of complete, one-third, and two-thirds.

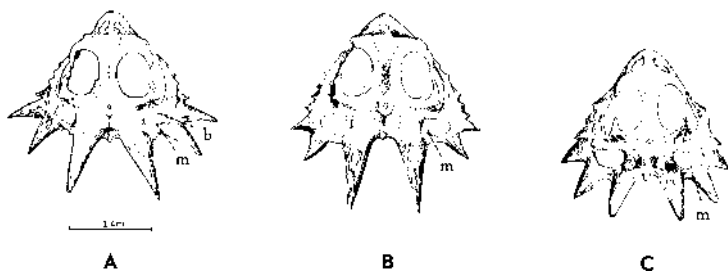


Figure 1. Skulls of horned lizards. A. *P. m'callii* (showing fossae partly occluded), B. *P. platyrhinos*, C. *P. coronatum blainvillii*. b, bony shelf; m, membrane covering the supratemporal fossae.

Although there is considerable variation within the adult age group, there is, nevertheless, a fair correlation between the degree of occlusion of the fossae and age. The single juvenile specimen (Fig. 2, A) in the series shows the least closure, approximately one-fourth. Seven (78 per cent) of the adults have two-thirds or greater occlusion, and of these, four have complete occlusion. The closure of the fossae by bone proceeds, in all probability, through ontogeny but at considerably different rates in different individuals. Degree of closure shows no correlation with sex in our small sample.

None of the additional seven species examined show bony growths within the membranes that limit the fossae. The fossae of *P. platyrhinos* are relatively smaller than those of the other species.

Tympanum and associated structures. In *P. platyrhinos* (Fig. 3, B) the columella auris consists of a bony proximal stapedial element and a cartilagenous extra-columellar element. The bony stapes is composed of a discoid portion resting in the fenestra ovalis and a translucent bony bar (the medio-stapedial element) connecting to the extra-columella lying largely within the tympanic membrane. This latter cartilagenous structure is composed of a central element and two processes. The first process is a small pyramidal

processus internus, which rests on the quadrate bone and acts as a fulcrum in sending vibrations to the inner ear. The second is the processus dorsalis lying longitudinally in the tympanum over the auditory cup or tympanic recess. The central portion of the extra-columella lies across the lower part of the tympanum. Although the tympanum is somewhat restricted by the depressor mandibulae muscle, it appears obvious that the ear of *P. platyrhinos* is functional.

In *P. m'callii* (Fig. 3, A) the effects of forward displacement of the depressor mandibulae muscle are at once apparent upon examination of the tympanum and columella. The tympanum is nearly covered by this muscle. When the depressor mandibulae is dissected away a degenerate tympanum is revealed. It appears as a slackened and much fenestrated connective tissue sheet lying over a very shallow tympanic recess. The mediostapedial bar is intact though it is thinner than that of *P. platyrhinos*. Medially the discoid portion of the stapes rests in the fenestra ovalis; distally it connects directly with the quadrate bone. The cartilagenous extra-columella has been reduced to a small finger-like projection connected to the degenerate tympanum by a few strands of connective tissue. The partial filling of the tympanic recess appears to proceed along with a general thickening of the bones in the base of the skull. Undoubtedly the tympanum of *P. m'callii* is not functional. However, the animal may perceive vibrations in the manner of snakes and salamanders (Hilton, 1949) due to the articulation of the mediostapedial portion of the columella with the quadrate bone.

When *P. m'callii* and *P. platyrhinos* are viewed laterally, it is immediately apparent that the head of *P. platyrhinos* is tilted at a considerably greater angle to the frontal (horizontal) plane than is that of *P. m'callii*. A straight line along the occipital spines and through the rostral scale, when intersected by another line along the supralabials, forms an angle of approximately 18 degrees in *P. m'callii*. This same angle is approximately 25 degrees in *P. platyrhinos*. In *P. coronatum* the angle is approximately 34 degrees.

In *P. m'callii* the cervicomandibularis muscle (used primarily to move the head from side to side and to depress it) is much lengthened and is also somewhat enlarged, compared to that of *P. platyrhinos*. The reduction of the angle of the head to the frontal plane and the enlargement of this muscle have "forced" the depressor mandibulae so far forward that the ear opening has been completely occluded. This occlusion is present to a lesser degree in *P. platyrhinos* and not at all in *P. coronatum* where the cervicomandibularis is still more vertically positioned. Hence, in this respect *P. platyrhinos* bridges the morphological gap between the condition found in *P. coronatum* and *P. m'callii*. Moreover, it has been our observation in field study of these forms that *P. platyrhinos* is also intermediate in habits and general habitat.

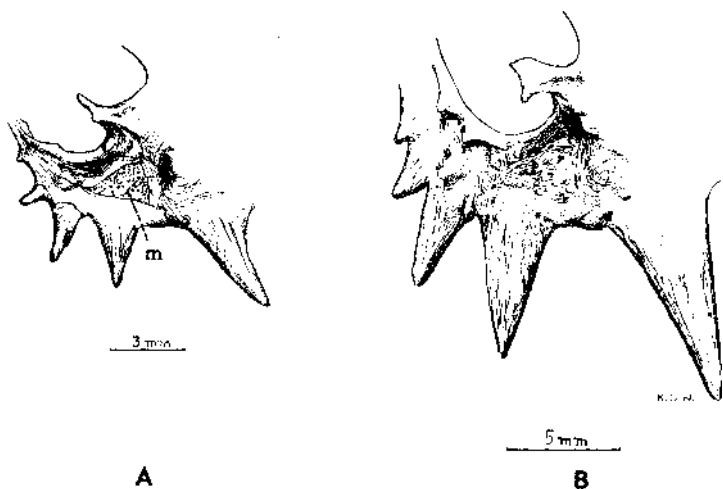


Figure 2. Supratemporal fossa of *P. m'callii*. A, juvenile; B, adult (showing completely occluded fossa).



Figure 3. Ear structure (tympanum partially dissected away). A. *P. m'callii*, B. *P. platyrhinos*. e, extracolumella; i, processus internus; m, mediostapedial bar; q, quadrate bone; s, discoid portion of stapes; t, tympanic membrane.

DISCUSSION

In *P. m'callii* closure of the supratemporal fossae, degeneration of the tympanum and extra-columella, and the musculature changes noted, appear to be adaptations to a sand-dwelling existence. *P. m'callii* is primarily an arenicolous form which employs burrowing to escape and to cover itself during periods of inactivity (Klauber, 1939; Norris, 1949). Since burrowing is accomplished in part by lateral movements of the head, it is not unexpected that the muscles producing such a movement should be enlarged. *P. m'callii* uses this same movement of the head during defense, to drive its needle-sharp head spines into its captor. With regard to the Amphisbaenidae, Camp (1923, p. 372) states that, "The cervicomandibularis has a broad insertion and, as in all strong burrowers, is enormously developed to act as a powerful depressor and lateral adductor of the head." The general strengthening of the base of the skull also seems explicable when one considers the burrowing habit. The closure of the fossae and the reduction in depth of the tympanic recess certainly serve to strengthen the posterior portion of the skull.

The cervicomandibularis muscle of *P. coronatum* lies nearly in the transverse plane, from its origin on the cervical vertebrae to its insertion on the mandible. This arrangement must produce only limited power for lateral movements of the head. On the other hand, the lengthened and enlarged cervicomandibularis of *P. m'callii* lies nearly in the frontal (horizontal) plane and is more effective in producing such burrowing movements. Tilting of the head and enlargement of the cervicomandibularis muscle in *P. m'callii* have served to "force" the depressor mandibulae muscle close under the occipital spines thus covering the tympanum. Degeneration of the tympanum and extra-columellar elements (through selection) was probably the result of such coverage. The attachment of the mediostapedial bar to the quadrate bone may be either a result of degeneration or a consequence of positive selection.

Malcolm A. Smith (1938) has made a study of auditory structures in several families of lacertilians in connection with the problem of the evolution of earlessness in snakes. Agamid genera having a naked tympanum are shown to possess auditory structures much like those described here for *Phrynosoma platyrhinos*. In agamids with a covered tympanic membrane, such as *Otocryptus*, *Ptyctolaemus*, *Phrynocephalus*, and *Phoxophrys*, the bony and cartilagenous structures of the middle ear remain intact. Regarding species lacking a tympanum Smith states (*loc. cit.*, p. 546):

"In the genera *Tympanocryptis*, *Aphanotis*, *Cophotis*, *Lyriocephalus*, and *Ceratophora* the tympanic membrane has disappeared, and its place is covered by muscle, an extension of the anterior branch of the *Depressor mandibulae* (text fig. 4), the extra-columella is reduced to a vestige projecting from the stapes, and the dorsal and ventral processes have become ossified and unite the stapes to the quadrate....."

This condition is very similar to that described here for *P. m'callii*, and that of *Holbrookia maculata* described by Smith (*loc. cit.*, p. 548).

The genera studied by Smith (*op. cit.*) show a gradation in auditory apparatus from the typical lactertilian condition to one closely approaching that of snakes. He states (p. 549):

"The reason for these retrogressive changes in the ear is not evident. They are happening in creatures that live an active life on the ground and in the trees, and should benefit by having good hearing powers

"An orthogenetic view seems to offer the only satisfactory explanation of the phenomenon. The acquisition of snake-like characters by the lizards is already well known. Elongation of the body and degeneration of the limbs have occurred in the Pygopodidae, the Anguidae, and in many genera of the Scincidae; the covering of the eye with a transparent disc in the Pygopodidae, the Lacertidae (*Cabrita*, *Ophisops*), and in the Scincidae (the Leiolopismids and *Ablepharus*). And now in the Agamidae and Iguanidae the changes in the ear."

Certainly the structural peculiarities of many reptiles are such that specialization toward ophidian morphology would follow certain environmental stresses, and this may be the "orthogenesis" of Malcolm Smith; but in its strictest sense (i. e., an evolutionary trend not guided by natural selection) orthogenesis certainly need not be called upon as an explanation of this trend. In all the cases noted by Smith where the tympanum and extra-columella were absent or degenerate, the auditory cup had been covered to some extent by the depressor mandibulae muscle. It seems possible that this degeneration has been the result of environmental stresses which, through selection, have brought about changes in the musculature surrounding the tympanum, as appears to have been the case with *P. m'callii*. When one considers the orientation of a snake's head in relation to its body, it is not at all surprising that the tympanum and extra-columella have been lost and the stapes attached to the quadrate bone during the transition from lacertilian posture.

Due to the variable nature of the supratemporal fossae of *P. m'callii* it is our opinion that its closure (occlusion by bone) is of little taxonomic importance with regard to the generic status of the species. The absence of the fossae, even if invariable, would not, alone, warrant recognition of a monotypic genus *Anota*. *P. m'callii* shows a great many similarities to other members of the genus *Phrynosoma* and but a few differences. Most of these differences appear to be adaptations to a specialized environment. The genus *Phrynosoma* is not recognized by the nature of the tympanum, the presence of head spines, or by the nature of the supratemporal fossae alone. Rather it is recognized by the aggregation of unique characteristics belonging to a group of species comprising an obviously natural evolutionary group. Simpson (1945, p. 23) states:

"What is deplorable in splitting is the tendency to raise the ranks of groups without need, that is, without gaining any practical advantage. One of the more evident symptoms of this tendency is the appearance of many monotypic groups in classification."

SUMMARY AND CONCLUSIONS

The supratemporal fossae of adult *Phrynosoma m'callii* are occluded in variable amount by shelves of bone extending inward from the three bones limiting the fossae. Ossification appears to proceed within the membranes which cover the fossae; the membranes are present in all species of *Phrynosoma* examined. The degree of bony occlusion appears to increase throughout ontogeny.

The degenerate tympanum of *P. m'callii* is obscured by the depressor mandibulae muscle. This muscle has been "pushed" forward with a lessening of the angle of the occipital horns to the frontal plane and with a lengthening and increase in size of the cervicomandibularis muscle. The tympanum appears to have become functionless.

It is suggested that the changes noted in *P. m'callii* have been produced in connection with the stresses engendered by the burrowing habit which is so marked in this primarily arenicolous form.

Similar changes have been noted in other lizard genera and in each case the depressor mandibulae muscle has encroached on or covered the tympanic recess. The middle ear of these lizards approximates the condition found in snakes. The condition of the middle ear of snakes may have been developed as the position of head and neck musculature was altered in change from lacertilian to ophidian head posture.

Phrynosoma m'callii, when all its characteristics are considered, falls close to the mode of the natural evolutionary group, *Phrynosoma*. To consider it as a monotypic genus (*Anota*) gains no practical advantage and means placing undue emphasis on its differences, resulting in obscuring its basic similarities. It is our opinion that it is desirable only to continue the present recognition of *m'callii* as a member of the genus *Phrynosoma*, as this genus is now understood.

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